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THAUMASTOPSALTRIA SMITHERSI, A NEW CICADA FROM NORTHERN QUEENSLAND WITH AN ANALYSIS OF ITS PHYLOGENETIC RELATIONSHIPS (HEMIPTERA: CICADIDAE: CICADETTINAE: CHLOROCYSTINI)

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Abstract

Thaumastopsaltria smithersi sp. n. is only the second species of *Thaumastopsaltria* Kirkaldy to be recorded from Australia. Its distinguishing features are documented together with notes on its distribution and habitat. A revised phylogeny for the genus is provided and the phylogenetic relationships of *T. smithersi* discussed.

Introduction

The genus *Thaumastopsaltria* Kirkaldy includes seven species found in Waigeo and Misoöl Islands, mainland New Guinea, D'Entrecasteaux Islands, New Britain, Umboi Island, northern Australia and, doubtfully, from Buka Island and Bougainville (de Boer 1992). The genus has recently been redefined and its distinguishing features summarised (Moulds 2012). *Thaumastopsaltria* belongs to the tribe Chlorocystini Distant, 1905 and a detailed analysis of relationships within the Chlorocystini was provided by de Boer (1995a).

The single previously described Australian species of *Thaumastopsaltria*, *T. globosa* (Distant), is known from along the eastern margin of Cape York Peninsula from Banks Island in Torres Strait to Daintree, and from Groote Eylandt, Northern Territory (Moulds 1990, as *T. glauca*, a synonym of *T. globosa*). A second species is described here, with its distribution confined to the rainforests south from Cooktown and with only a marginal overlap with that of *T. globosa*. Phylogenetic relationships of this new species are discussed below and a revised phylogeny for the genus is provided.

Terminology for morphological features follows Moulds (2005, 2012) and for higher classification that of Moulds (2005). The following abbreviations have been used for collections housing specimens: *AE*, collection of A. Ewart, Golden Beach; *AM*, Australian Museum, Sydney; *ANIC*, Australian National Insect Collection, Canberra; *LP*, collection of Lindsay Popple, Brisbane; *MSM*, collection of M.S. Moulds, Kuranda; *ML*, collection of Mark Lane, Atherton; *QM*, Queensland Museum, Brisbane.

Thaumastopsaltria smithersi **sp. n.**

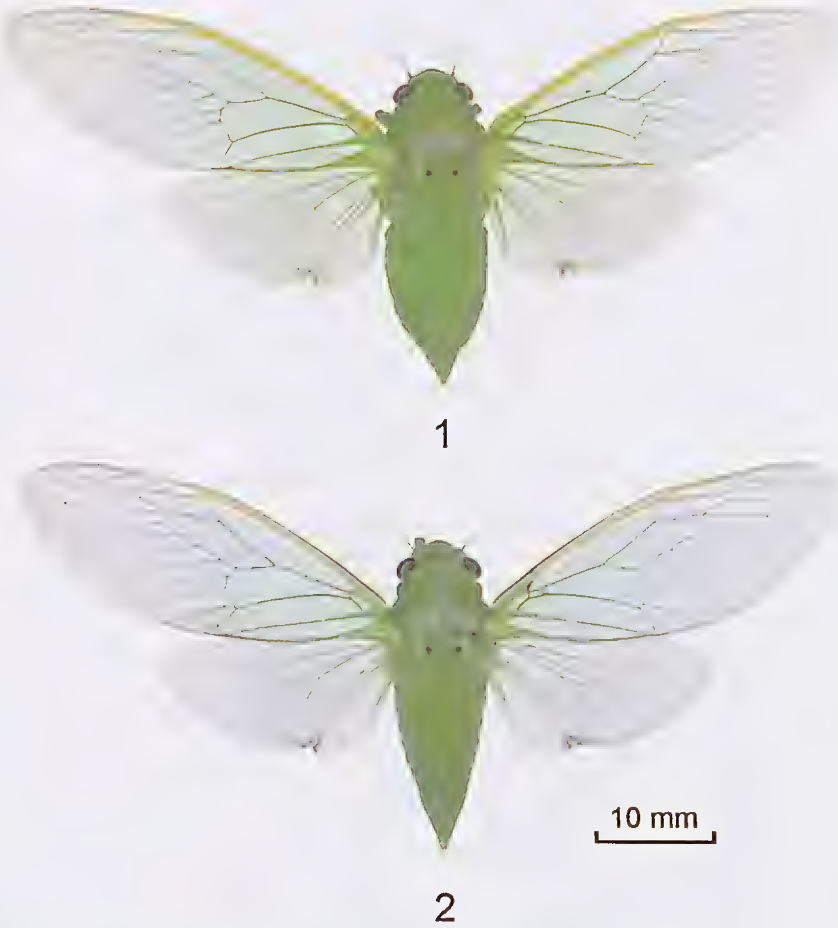
(Figs 1-9)

Type material. Holotype ♂, QUEENSLAND: 6 Victor Pl., Kuranda, 16°48'50"S 145°38'36"E, 18.xii.2008, Hill, Marshall, Moulds (AM). *Paratypes* (all northeastern Queensland): 1 ♂, 2 ♀♀, Kuranda, 10.i.1983, 7.ii.1982, 3.iii.1982, W.N.B. Quick; 1 ♀, 16.08S 145.26E, 2.5 km WSW of Noah Head, Cape Tribulation NP, 'Marrdja Botanical Walk', 2.xi.1993, D.C.F. Rentz & W.L. Lowe, stop 11 (ANIC); 1 ♂, 1 ♀, nr

The Crater, 20 km S of Atherton, 21,29.xi.1987, D.A. Lane (AE); 1 ♂, 1 ♀, The Creator, near Herberton, 3.i.1967, D.K. McAlpine & G. Holloway (AM); 1 ♂, 1 ♀, nr The Crater, 20 km S of Atherton, 29.xi.1987, D.A. Lane (LP); 5 ♂♂, 1 ♀, Longlands Gap, 20 km south Atherton, 19.xii.2001, D.A. Lane (ML); 1 ♀, Mt Hartley, nr Rossville, S of Cooktown, 1.i.1984, M.S. & B.J. Moulds; 1 ♀, Gap Ck, Mt Finlayson Rg, S of Cooktown, 10.ii.1982, M.S. & B.J. Moulds; 2 ♂♂, Windsor Tableland, NW of Mossman, 16.i.1988, M.S. & B.J. Moulds; 1 ♀, Mt Lewis via Julatten, 21.xii.2009, Gilligan & Epstein; 5 ♂♂, 7 ♀♀, Kuranda (Top of the Range), 19 Butler Dr., 335 m elev., 16°48'S 145°38'E, 15-30.x.2004, 1-15.xi.2004, 1-15.xi.2006, 1-15.xii.2005, 1-15.xii.2007, 16-31.x.2008, 1-15.xi.2008, 16-30.xi.2008, 1-15.xii.2008, 1-15.ii.2009, 1-15.i.2010, D.C.F. Rentz; 1 ♀, Kuranda, 10.xi.1987, 7.xii.1987, J. Hasenpusch; 1 ♂ (genitalia prep. THE3), Kuranda, xii.1985, R. Straatman; 1 ♂, Kuranda, 5.ii.1987, R. Straatman; 1 ♂, Whitfield Rg, nr Cairns, 2.xii.1986, M.S. & B.J. Moulds; 1 ♂, Hugh Nelson Range, 20 km S of Atherton, 18.xi.1990, D.A. Lane; 2 ♂♂ (one genitalia prep. THE4), 2 ♀♀, nr The Crater, 20 km S of Atherton, 21,29.xi.1987, D.A. Lane; 1 ♂, The Crater, Atherton Tableland, 24.xii.2009, Gilligan & Epstein; 1 ♂, 'Chowchilla', Westcott Rd, Topaz, approx. 15 km SSE of Malanda, 18.xi.1990, W.T. Cooper; 1 ♀, 'Chowchilla', Westcott Rd, Topaz, approx. 15 km SSE of Malanda, 25.xi.2000, W.T. Cooper; 1 ♀, Bartle Frere, 27.xii.2000, A. Polak; 1 ♀, Ravenshoe, i.1986, S. Lamond; 4 ♂♂ (one genitalia prep. THE2), 3 ♀♀, Polly Ck, Garradunga N of Innisfail, 20.xi.1987, 23.xi.1996, 20,23.x.2006, 9.i.2008, 12.xi.2008, J. Hasenpusch (MSM); 1 ♂, 1 ♀, Kuranda (Top of the Range), 19 Butler Dr., 335 m elev., 16°48'S 145°38'E, 1-15.xii.2007, 1-15.xii.2008, D.C.F. Rentz; 1 ♂, Kirrama Range, Douglas Ck Rd, 800 m, 7-12.xii.1986, Monteith, Thompson & Hamlet (QM).

Distinguishing features. Distinguished from all other Australian cicadas in having 12 apical cells in the forewing (11 or 13 if aberrant, but usually so only in one wing) and no subapical cells. Distinguished from *T. globosa* by the pair of black thoracic spots located near the ends of the anterior arms of the cruciform elevation highlighting the scutal depressions (absent on *T. globosa*), and the widely spaced ocelli that have the distance between them considerably greater than their diameter (those of *T. globosa* have the ocelli close together, closer than their diameter). The male aedeagus is unique within *Thaumastopsaltria* in having the apical gonopore sloping backwards along the dorsal surface and terminating in a small dorsal crest (Fig. 5); other species have a gonopore either sloping backwards along the ventral surface or not sloping at all so that the aedeagus in lateral view has the apex square.

Description. Male (Figs 1, 3-8). Head light green, tending pastel in tone, paler below than above, about as wide as lateral margins of pronotal collar; eyes tan tending a little reddish; ocelli small and widely separated with the distance between them much greater than their diameter; postclypeus and anteclypeus a little paler than dorsal surface of head; postclypeus in lateral view barely obtusely bent; in ventral view (Fig. 3) rostrum very pale brown with darker tip, reaching near to bases of hind coxae. Thorax similar in colour to head. Pronotum sometimes with hints of very pale orange centrally; prothoracic collar mostly very pale orange across dorsal surface but otherwise light green; paratnota rounded. Mesonotum usually with a very



Figs 1-2. *Thaumastopsaltria smithersi* sp. n.: (1) holotype male, dorsal view; (2) paratype female, 19 Butler Drive, Kuranda, dorsal view.

pale orange fascia either side of midline aligned with distal ends of anterior arms of cruciform elevation; scutal depressions highlighted as black spots. Metathorax similar in colour to pro- and mesothorax. Wings (Figs 1-2) hyaline. Forewing with 12 apical cells (often 11 or 13 if aberrant but if so usually only in one wing); veins very fine, costal margin very pale yellowish orange, veins otherwise pale green or black. Hind wing with seven apical cells; distinct infuscation at distal ends of veins 1A and 2A spreading onto wing margin; veins mostly very pale green but some pale brown or very pale orange. Legs very pale green becoming very pale yellowish brown distally from about mid length of tibia. Timbals (Fig. 4) with seven long ribs spanning width of timbal plate and seven short ribs, the ribs occupying most of timbal area; timbal plate narrow and mostly concealed. Opercula (Fig. 3) very pale green, covering a little less than half tympanal cavity, transversely broad and broadly rounded towards midline, clearly separated exposing most of sternite I. Abdomen dorsally similar in colour to head and thorax, paler ventrally, sometimes tending very pale bluish green and often with hints of very pale brown around distal midline and sternite VIII.

Genitalia (Figs 5-8). Pygofer in ventral view (Fig. 8) with cavity tapering towards base, in some individuals forming a distinct 'V' shape; pygofer upper and basal lobes in lateral view (Fig. 7) weakly developed and broadly rounded. Claspers well developed, claw-like, their apices slightly diverging and slightly down-turned. Uncus degenerate, barely discernible. Aedeagus with theca (Fig. 5) almost cylindrical, gradually tapering towards apex, straight or gently curved in a shallow arc; gonopore apical but sloping backwards along dorsal surface of theca, the opening at its proximal end narrowing and forming a small crest in lateral view; basal plate almost rounded in dorsal view (Fig. 6), stepped in lateral view (Fig. 5).

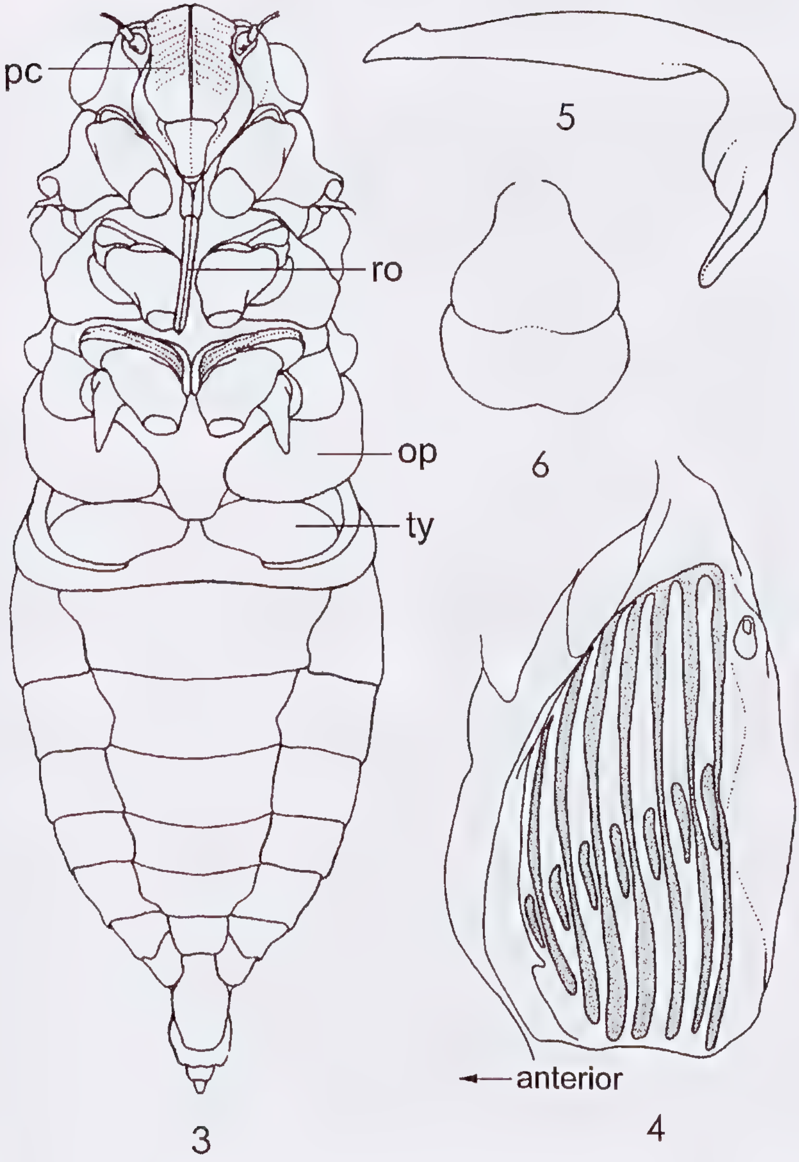
Female (Fig. 2). Similar to male. Abdominal segment 9 uniformly pale green, along dorsal midline just a little longer than abdominal tergites 7 and 8 combined; ovipositor sheath terminating about level with caudal beak; caudal beak sharply pointed.

Measurements. Range and mean (in mm) for 10 males and 10 females, including smallest and largest available specimens. *Body length*: male 21.4-27.2 (25.1); female 21.0-25.5 (23.3). *Head width (including eyes)*: male 5.7-6.7 (6.2); female 5.9-6.9 (6.5). *Pronotum width (across lateral angles)*: male 6.7-8.8 (7.7); female 6.7-8.7 (7.9). *Forewing length*: male 28.3-37.3 (32.3); female 27.5-35.1 (31.4). *Forewing width*: male 10.2-13.8 (11.9); female 9.7-13.1 (11.5). *Forewing ratio width/length*: male 2.7 ± 0.1; female 2.7 ± 0.1.

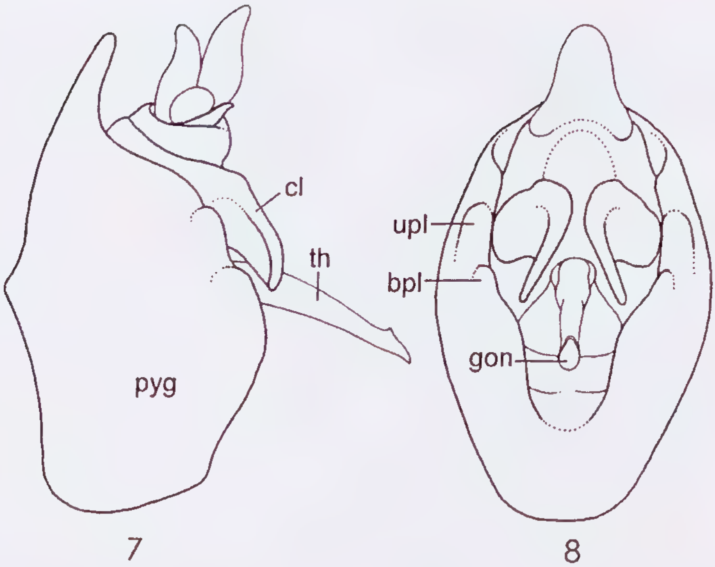
Etymology. Named in memory of Dr Courtenay Smithers, a friend and mentor, past Curator of Insects, Principal Curator and Deputy Director of the Australian Museum. Courtenay had broad interests in entomology covering most Orders and his extensive publications contributed significantly to our knowledge of Australian insects.

Song. Singing occurs at dusk and is a high pitched, whistle-like, continuous call.

Distribution and habitat (Fig. 10). Northeastern Queensland, south from Mount Hartley (south of Cooktown near Rossville) to the Kirrama Range (north-west of Cardwell). Most records are from mountain areas between about 300 m and 800 m but there are records from much lower altitudes, including Gap Ck south of Cooktown at 40 m, Marrdja Botanical Walk, Cape Tribulation at 21 m and Polly Ck, Garradunga at 25 m. The species has been found only in rainforest. Adults have been taken from mid October to mid February but are most common during November and December.



Figs 3-6. *Thaumastopsaltria smithersi* sp. n.: (3) ventral view of body; (4) left timbal showing ribs; (5) aedeagus in lateral view; (6) basal plate of aedeagus in dorsal view, apex at bottom. *op* operculum; *pc* postclypeus; *ro* rostrum; *ty* tympanum.



Figs 7-8. *Thaumastopsaltria smithersi* sp. n., male genitalia: (7) lateral view; (8) ventral view with claspers spread apart. *bpl* basal pygofer lobe; *cl* clasper; *gon* gonopore of theca; *pyg* pygofer; *th* theca of aedeagus; *upl* upper pygofer lobe.

Phylogenetic relationships

De Boer (1995a) presented a cladistic analysis based on morphological characters and incorporating all known species of the tribe Chlorocystini. He found 600 equally parsimonious trees. The 50% majority rule tree for these 600 trees was found to contain nearly all previously recognized genera and species groups as monophyletic groups and was chosen by de Boer as the preferred tree showing relationships. De Boer's cladistic analysis has been adopted here to determine the phylogenetic position of *T. smithersi* sp. n. within the genus *Thaumastopsaltria*. A cladogram was reconstructed from de Boer's data set retaining only those characters suggesting phylogenetic relationships within *Thaumastopsaltria* and the outgroup. De Boer found that species of the genus *Mirabilopsaltria* de Boer were sister to those of *Thaumastopsaltria*. *Mirabilopsaltria globulata* de Boer and *M. humilis* (Blöte) were chosen as outgroup taxa. Character and state numbers used by de Boer (1995a) were retained to allow direct comparison with his analysis.

Data were analysed using the heuristic search parsimony algorithms implemented with PAUP* version 4.0b2 (Swofford 1998). Tree searches utilized the tree bisection reconnection algorithm (TBR) conducting 1,000 random addition searches (RAS) starting from random trees; other settings were left at their default values. All characters were unweighted and all multistate characters were treated as unordered. Unknown character states were scored as '?'. The matrix of species and assigned states is given in Table 1, followed by the characters and character states used, adopted from de Boer (1995a) using his character numbers and states but with minor modification as stated in the notes below relevant characters.

Table 1. Character matrix for the eight known species of *Thaumastopsaltria* and two species of *Mirabilopsaltria* used in the parsimony analysis (from de Boer 1995a). Missing data and character states unknown are scored as '?' Character numbers are those used by de Boer in his larger analysis of the Chlorocystini [reading downwards in heading]. However, character states have been renumbered sequentially from zero for the purpose of the current analysis in order to elucidate plesiomorphic states.

Species	00000 01122 52724	00000 33345 23514	00000 66667 15695	00011 89900 20503	11111 22344 09125	111 555 023
Mirabilopsaltria humilis (Blöte)	00000	00000	00000	00000	00000	000
Mirabilopsaltria globulata de Boer	00001	11110	10000	00011	00000	010
Thaumastopsaltria adipata (Stål)	10110	0120?	01012	00111	10100	0??
Thaumastopsaltria pneumatica de Boer	11102	01201	01011	01111	10101	020
Thaumastopsaltria spelunca de Boer	10112	11110	10011	11110	02211	120
Thaumastopsaltria globosa (Distant)	10102	11102	11112	11100	02211	121
Thaumastopsaltria sicula de Boer	10100	00010	10011	01100	02011	120
Thaumastopsaltria lanceola de Boer	10102	11000	01112	10100	01002	021
Thaumastopsaltria sarissa de Boer	11102	11000	01112	11101	01001	020
Thaumastopsaltria smithersi sp. n.	11103	00201	11?12	10101	02020	201

Characters and character states

005. *Postclypeus in lateral view*: (1) not swollen; (4) protruding in obtuse angle.

012. *Distance between lateral ocelli*: (1) about equal to distance between lateral ocellus and eye; (2) generally slightly larger than distance between lateral ocellus and eye.

017. *Paranotum* (*anterolateral side of pronotal collar*): (1) rounded; (4) forming continuous ridge.

022. *Proximal spine of foreleg*: (1) not shorter than distance to middle spine; (2) distinctly shorter than distance to middle spine.

024. *Colour of forewing*: (1) hyaline, completely without colour; (2) opaque greenish or reddish; (3) slightly reddish but still hyaline; (5) slightly greenish but still hyaline.

NOTE: De Boer listed four states for this character but his state 4 was not relevant to this analysis and is omitted. However, another state is here added (state 5) to accommodate the unique forewing colour of *T. smithersi*.

032. *Subapical cells of forewing*: (1) absent; (2) present but not forming a continuous band.

033. *Base of first apical area of forewing*: (1) distally of base of third apical area; (3) distinctly proximally of base of third apical area.

035. *Number of apical cells in hind wing*: (1) six; (3) six or seven; (4) seven or more.

NOTE: It is not clear why de Boer did not designate discrete character states. Examination of material available to me suggests that some species have either six or seven hind wing apical cells (often on the same specimen), while other species consistently have either six or seven or more; this is the presumed interpretation adopted here when scoring *T. smithersi*.

041. *Timbal cavity*: (1) broad; (2) narrow.

054. *Distal part of female operculum*: (1) rectangular oblong; (2) trapezoid; (3) narrow sickle-shaped.

061. *Second tergite of male*: (1) forming a distinct ridge along timbal cavity; (2) not forming a distinct ridge along timbal cavity.

NOTE: The scoring of this character had been accidentally reversed in de Boer (1995a).

065. *Male auditory capsule*: (1) swollen and protruding; (2) not swollen and not protruding.

066. *Male pygofer and 9th sternite*: (1) resting on 8th sternite; (2) elevated respective to 8th sternite.

069. *Male pygofer*: (1) not curved to ventral position; (2) curved to ventral position on abdomen.

075. *Apex of male dorsal beak*: (2) rounded; (3) truncate or weakly concave; (5) broadly rounded.

NOTE: The scoring of *T. smithersi* for these subjective character states was done by comparing the dorsal beak of *smithersi* with other available material and adopting the scoring of the most similar species.

082. *Protuberance on lateral lobe of male pygofer*: (1) not triangularly swollen; (2) triangularly swollen.

090. *Male pygofer*: (1) not swollen at ventral margin; (2) swollen at ventral margin.

095. *Ventral half of male pygofer opening*: (1) triangular and pointed; (2) broad and rounded.

100. *Clasper*: (1) strongly bent and hook-shaped; (2) nearly straight and posteriorly directed.

103. *Clasper*: (1) parallel; (2) diverging towards apices.

120. *Dorsal edge of clasper*: (1) not curved around aedeagus; (5) globularly rounded.

129. *Clasper*: (1) without ventromedial protuberance; (2) with broad and laminiform ventromedial protuberance; (3) with narrow and spiny ventromedial protuberance.

131. *Clasper*: (1) without lateral process; (2) with lobate lateral process; (3) with lateral thorn.

142. *Apical part of aedeagus*: (1) not abruptly narrowing; (2) abruptly narrowing and upcurved; (4) abruptly narrowing on dorsal surface.

NOTE: De Boer listed three states for this character but state 3 was not relevant to this analysis and is omitted. However, another state is here added (state 4) to accommodate the unique aedeagus of *T. smithersi*.

145. *Aedeagus*: (1) without dorsal crest; (2) with single dorsal crest; (3) with paired dorsal crests.

150. *Aedeagal pore*: (3) apically pointed but not widening proximally; (5) rounded; (6) apically wide and narrowing proximally.

NOTE: An additional state (state 6) is here added to accommodate the unique aedeagus of *T. smithersi*.

152. *Ovipositor sheaths*: (1) reaching to apex of dorsal beak; (2) reaching just beyond apex of dorsal beak; (3) reaching far beyond apex of dorsal beak.

153. *Apex of female dorsal beak*: (1) sharply pointed; (2) broadly rounded.

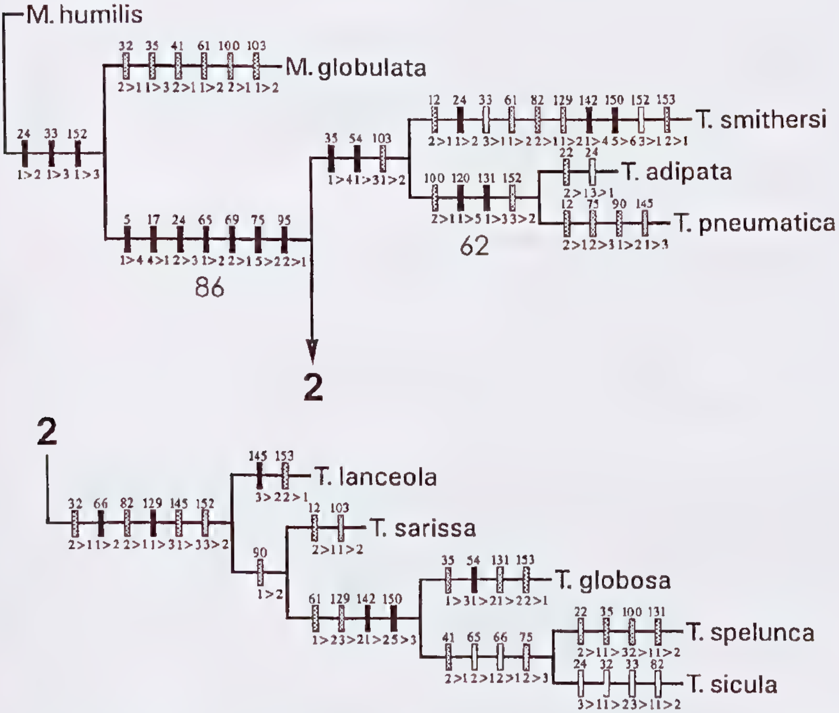


Fig. 9. The single most parsimonious tree derived using the procedures described in the text above (length 66, CI 57, RI 61) from an analysis of all *Thaumastopsaltria* species, employing *Mirabilopsaltria humilis* and *M. globulata* as outgroups, with all characters unordered and equally weighted. Numbers at nodes are bootstrap values >50% from 1,000 replications. Character transformations (generated using Clados) are represented by black bars = non-homoplasious forward changes; grey bars = homoplasious forward changes; and white bars = reversals (whether homoplasious or not). The analysis was run using the data set in Table 1 and state numbers modified (after analysis) to correspond with those used by de Boer (1995a).

Results from running de Boer's (1995a) reduced data set produced three equally parsimonious trees. However, by omitting de Boer's homoplasious character (character 103) from the analysis only one shortest tree was obtained. This tree was identical in topology to de Boer's 50% majority rule tree for the genus *Thaumastopsaltria*. *T. smithersi* sp. n. was then scored and the data added to the data set and the analysis re-run. Three additional character states were added to accommodate the variant forewing colour of *T. smithersi* (state 3 in character 24) and unique morphology of the aedeagus (state 2 in character 142 and state 2 in character 150) (Table 1). Three equally parsimonious trees were obtained but the relationships of *T. smithersi* were largely inconclusive. However, by again eliminating de Boer's character 103, just a single tree (Fig. 9) resulted, which was fully resolved and topographically similar to de Boer's 50% majority rule tree.

Although the single tree obtained here agrees with that of de Boer's 50% majority rule tree, it should be kept in mind that both trees are based on the same data set. Only the node distinguishing *Thaumastopsaltria* and one internal node are well supported statistically. Molecular data is currently unavailable for *Thaumastopsaltria* species but such data may provide confidence for internal nodes.

Relationships of *Thaumastopsaltria smithersi* sp. n.

The fully resolved tree obtained (Fig. 9) shows that *T. smithersi* sp. n. forms a monophyletic group together with *T. adipata* (Stål) (known from just a single specimen from Misoöl Island) + *T. pneumatica* de Boer (known only from Mt Dayman in eastern Papua New Guinea). This group of three is sister to all other *Thaumastopsaltria* species, including the only other Australian species, *T. globosa* (Distant).

Thaumastopsaltria globosa has a wide distribution throughout southern parts of Papua New Guinea, eastern Queensland south to Daintree, and Groote Eylandt on the Northern Territory side of the Gulf of Carpentaria (Fig. 10), a distribution accounted for when sea levels were much lower during several Pliocene-Pleistocene ice ages (between 5-3 and 0.01 Mya), when Queensland was connected to New Guinea via a land bridge and the Gulf of Carpentaria was largely dry (Pigram and Davies 1987, de Boer 1995b). *T. globosa* is not a wet rainforest species and would not have been inhibited in its spread by this specific habitat requirement. In contrast, *T. smithersi* is restricted to wet tropical rainforest between Cooktown and Cardwell (Fig. 10), a habitat that would have shrunk during those past ice ages when conditions were much dryer (Hopkins *et al.* 1993).

It is difficult to explain how *T. smithersi* could have become so isolated from its New Guinean sister species, none of which now inhabit the southern regions of that large island anywhere near Australia. This isolation must have originated a long time ago, possibly as long as 25 Mya when other, now endemic, Australian Chlorocystini are thought to have entered Australia following the Sepik Arc collision (Daly *et al.* 1991, de Boer 1995b).

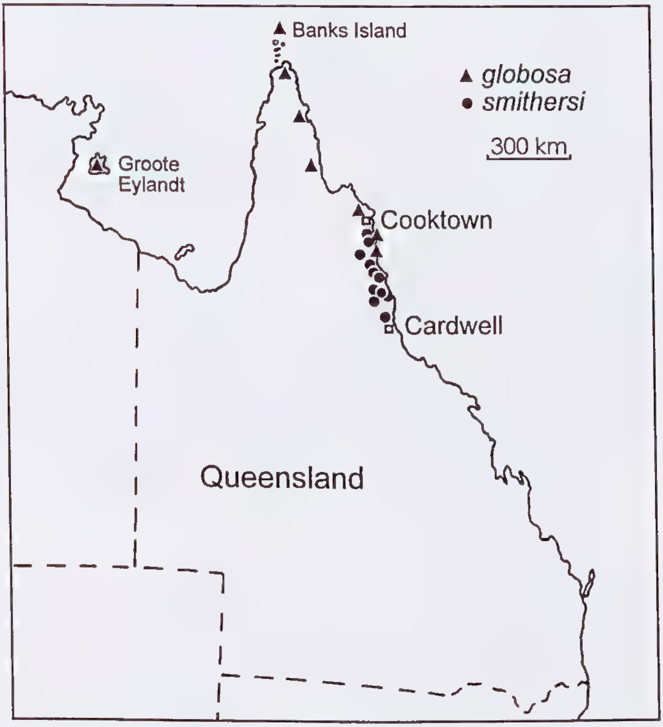


Fig. 10. Distribution of *Thaumastopsaltria smithersi* sp. n. and *T. globosa*.

On the monophyly of *Thaumastopsaltria* Kirkaldy, 1900

De Boer (1992) distinguished *Thaumastopsaltria* on the basis of the shape of the postclypeus and long female ovipositor. The postclypeus in lateral view is obtusely bent at about mid point and thereafter straight to anteclypeus, and the lateral margins show several rows of short parallel ridges. Further, de Boer pointed out that the male pygofer upper lobes in most species are distinctly inflated towards the ventral margin, a feature believed to be unique within *Thaumastopsaltria*.

The monophyly of *Thaumastopsaltria* (incorporating *T. smithersi* sp. n.) is strongly supported in the cladistic analysis by seven non-homoplasious synapomorphies and a bootstrap of 86%. However, three of those synapomorphies have one or more reversals within *Thaumastopsaltria* (characters 24, 65 and 75). The combination of the remaining four synapomorphies (characters 5, 17, 69 and 95 unambiguously define the genus as follows: (a) shape of the postclypeus as mentioned above; (b) paranotum (the lateral side of pronotal collar) rounded; (c) the male pygofer not curved to ventral position; (d) the ventral half of pygofer opening triangular and pointed rather than broad and rounded. The combination of these four synapomorphies clearly characterises the genus although some of these may have been homoplasious in de Boer's (1995a) large analysis (shared with nodes in other parts of his tree). As de Boer (1992) pointed out, the shape of the postclypeus appears to be the most reliable distinguishing feature. Note that the long female ovipositor, considered by de Boer as a defining attribute for the genus, is not included among the seven synapomorphies identified by the present cladistic analysis (character 152). This is because the ovipositor of *T. smithersi* is short, terminating at about the distal end of abdominal segment 9 and, as *T. smithersi* is near the base of the tree, the analysis treats the character as homoplasious.

Acknowledgements

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References

BOER, A.J. de 1992. The taxonomy and biogeography of the genus *Thaumastopsaltria* Kirkaldy, 1900 (Homoptera, Tibicinidae). *Beaufortia* **43**: 17-44.

BOER, A.J. de 1995a. The phylogeny and taxonomic status of the Chlorocystini (Homoptera, Tibicinidae). *Bijdragen tot de Dierkunde* **65**: 201-231.

BOER, A.J. de 1995b. Islands and cicadas adrift in the west-Pacific. Biogeographic patterns related to plate tectonics. *Tijdschrift voor Entomologie* **138**: 169-244.

DALY, M.C., COOPER, M.A., WILSON, I., SMITH, D.G. and HOOPER, B.G.D. 1991. Cenozoic plate tectonics and basin evolution in Indonesia. *Marine and Petroleum Geology* **8**: 1-21.

HOPKINS, M.S., ASH, J., GRAHAM, A.W., HEAD J. and HEWETT R.K. 1993. Charcoal evidence of the spatial extent of the *Eucalyptus* woodland expansion and rainforest contractions in North Queensland during the late Pleistocene. *Journal of Biogeography* **20**: 357-372.

MOULDS, M.S. 1990. *Australian cicadas*. New South Wales University Press, Kensington; 217 pp, 24 pls.

MOULDS, M.S. 2005. An appraisal of the higher classification of cicadas (Hemiptera: Cicadoidea) with special reference to the Australian fauna. *Records of the Australian Museum* **57**: 375-446. *http://dx.doi.org/10.3853/j.0067-1975.57.2005.1447*

MOULDS, M.S. 2012. A review of the genera of Australian cicadas (Hemiptera: Cicadoidea). *Zootaxa* **3287**: 1-262. *http://mapress.com/zootaxa/2012/f/zt03287p262.pdf*

PIGRAM, C.J. and DAVIES, P.J. 1987. Terranes and the accretion history of the New Guinea orogen. *BMR Journal of Australian Geology and Geophysics* **10**: 193-212.

SWOFFORD, D.L. 1998. PAUP* 4.0. *Phylogenetic analysis using parsimony.* Beta version 4.0d100. Smithsonian Institution.